AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 111:221–244 (2000)

Taxonomic and Functional Aspects of the Patterning of Enamel Thickness Distribution in Extant Large-Bodied Hominoids

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KEY WORDS enamel thickness; maxillary molars; modern humans; great apes; mastication; tooth function; diet; enamel development

ABSTRACT One of the few uncontested viewpoints in studies of enamel thickness is that the molars of the African apes, *Pan* and *Gorilla,* possess "thin" enamel, while *Pongo* and modern humans possess varying degrees of "thick" enamel, even when interspecific differences in overall body or tooth size are taken into account. Such studies focus primarily on estimates of the total volume of enamel relative to tooth size (i.e., "relative" enamel thickness), as this is thought to bear directly on questions concerning dietary proclivities and phylogenetic relationships. Only recently have studies shifted focus to examining differences in the distribution of enamel across the tooth crown, i.e., the patterning of enamel thickness, as this may contribute to more refined models of tooth function and dietary adaptations in extant hominoids. Additionally, this feature has been suggested to be a reliable indicator of taxonomic affinity in early hominins, though no study has specifically addressed whether species-specific patterns exist among known phena.

The aims of this paper were to test more explicitly whether enamel thickness patterning provides valuable taxonomic, functional, and/or phylogenetic information for maxillary molars of large-bodied extant hominoids. A series of seven linear enamel thickness measurements was recorded in the plane of the mesial cusps in cross sections of a total of 62 maxillary molars of *P. troglodytes, G. gorilla, P. pygmaeus,* and *H. sapiens* to estimate the patterning of enamel thickness distribution. Results from a discriminant function analysis reveal that, overall, this trait reclassifies extant hominoid maxillary molars with 90% accuracy: 100% of extant *Homo,* 75.0% of *Pongo,* 83.3% of *Pan,* and 66.7% of *Gorilla* are reclassified correctly, indicating that this feature possesses a strong taxonomic signal. Furthermore, differences in the structure of the enamel cap are evident among hominoids: modern humans differ from *Pongo* in possessing proportionally thicker enamel in areas of the crown associated with shearing activity; *Pan* molars are better designed than those of *Gorilla* for generating a greater component of crushing/grinding loads. Thus, African ape molars are structurally dissimilar, even though they are both considered to belong to a morphologically homogeneous "thin-enameled" group. Simple developmental mechanisms can be invoked to explain the sometimes subtle differences in the achievement of adult morphology. For instance, human and

Grant sponsor: L.S.B. Leakey Foundation; Grant sponsor: Boise Fund, Oxford University; Grant sponsor: Sigma Xi; Grant sponsor: Leverhulme Trust; Grant sponsor: Dean's Dissertation Fellowship, Washington University.

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Received 4 January 1999; accepted 26 August 1999.

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orangutan molar cusps possess a similar degree of enamel thickness, but the possibility exists that despite similarities in morphology, each species follows a different sequence of secretory activity of enamel to achieve the final, albeit similar, degree of enamel thickness. Such a finding would suggest that the shared possession of "thick" or "thin" enamel among species may be phylogenetically uninformative, as it would not represent a developmental synapomorphy. Am J Phys Anthropol 111:221–244, 2000. © 2000 Wiley-Liss, Inc.

Increases in the amount of dental tissue available for wear enhance the functional durability and hence the lifetime of the dentition. One means of providing more dental tissue is by increasing the amount of enamel over the surface of the tooth. This can be achieved by enlarging the surface area of dentine over which the enamel forms, requiring an increase in the number of active ameloblasts at any one time, or by producing thicker enamel, which requires either lengthening the secretory phase or increasing the secretory rate of individual ameloblasts. Several groups of living and extinct animals are known to have independently acquired the condition of thickened enamel, including the suids, *Potamochoerus* and *Phacochoerus* (Hatley and Kappleman, 1980), some pantolestids and dimylids (Schmidt-Kittler, 1973; Savage and Long, 1976), manatees and desmostylians (Vanderhoff, 1937; Domning, 1982), sthenurine kangaroos (Janis and Fortelius, 1988), the mollusc-eating sea-otter (Ewer, 1973), and species of the primate genera *Daubentonia, Cebus, Cercocebus, Theropithecus, Pongo, Sivapithecus, Ouranopithecus, Australopithecus, Paranthropus,* and *Homo* (e.g., Robinson, 1956; Jolly, 1970; Gantt, 1977; Kay, 1981; Martin, 1983; Grine and Martin, 1988; Andrews and Martin, 1991; Conroy, 1991; Macho and Thackeray, 1992; Shellis et al., 1998). This study investigates the functional and taxonomic utility of enamel thickness distribution among living large-bodied hominoids.

BACKGROUND

The total amount of enamel overlying the dentine core of molars is thought to bear directly on questions concerning dietary regimens and the biomechanical constraints of the masticatory apparatus (e.g., maximum bite force), and has thus been the focus of many recent paleoanthropological studies. Generally speaking, extant large-bodied hominoids are characterized by both thick- and thin-enameled species (Molnar and Gantt, 1977; Martin, 1983, 1985; Beynon et al., 1991), while most fossil hominins possess relatively thicker enamel (e.g., Robinson, 1956; Beynon and Wood, 1986; Grine and Martin, 1988; Conroy, 1991; Macho and Thackeray, 1992; Schwartz, 1997; Shellis et al., 1998). Observed differences in the thickness of enamel among these taxa have usually been regarded as evolutionary responses to differing diets (Robinson, 1956; Jolly, 1970; Simons, 1976; Kay, 1981; Gantt, 1983; Shellis and Hiiemae, 1986; Andrews and Martin, 1991). In a very general sense, animals that habitually feed upon hard food objects such as nuts and seeds possess thick molar enamel, while those animals that are primarily folivores possess molars characterized by thin enamel. Thinner molar enamel results in earlier exposure of the dentine at the cusp tips. This configuration is advantageous since it results in sharp crests of enamel better suited to shear tough, fibrous vegetation. On the contrary, thick enamel wears in such a way as to provide a more flattened surface that is highly efficient for grinding and allows the tooth to function longer in extreme wear conditions.

Some of the earliest estimates of enamel thickness were based on examinations of cusp topography. Butler (1956) first recognized the connection between occlusal morphology and enamel thickness, and proposed that differences in the occlusal features of a tooth (e.g., cuspal morphology) were more heavily influenced by local changes in the thickness of enamel rather than in the underlying dentine. High cusp relief and sharp enamel ridges, for example, implied the presence of a thin layer of enamel that

accurately portrayed the topography of the underlying dentine surface, while more rounded, bulbous cusps indicated thicker enamel. This scheme provided a set of criteria for constructing the comparative dichotomy of "thin-enameled" vs. "thick-enameled" teeth. Subsequently, data on cusp morphology were viewed in conjunction with observations on the pattern of occlusal wear. For instance, species such as "*Ramapithecus*" (= *Sivapithecus*) and *Australopithecus* revealed little dentine exposure, even with heavy wear. This was taken as indirect evidence for thickened molar enamel, which led to the inclusion of "*Ramapithecus*" as a putative ancestor of the hominin lineage (Simons and Pilbeam, 1972). The purported hominin status of "*Ramapithecus*" was bolstered by the recognition of thick enamel as being part of a suite of characteristics that defined hominins within the Hominoidea (Jolly, 1970).

Comparative studies on enamel thickness

Though often cited as a taxonomically informative character, the use of enamel thickness for taxonomy was difficult, as few comparative data existed. In an attempt to fill this gap, enamel thickness was surveyed in cercopithecoid and hominoid dental specimens relevant to an understanding of its functional and phyletic importance (Gantt, 1977). Subsequently, Kay (1981) examined the relationships among enamel thickness, molar occlusal structure, and foraging strategy in extant anthropoids and several thick-enameled Miocene apes. He constructed a measure of "relative enamel thickness" for comparative purposes, using the thickness of enamel along the slope of the M_2 cristid obliquid. However, it should be kept in mind that the use of a single figure to express an average enamel thickness is problematic; the only optimum measure for comparative purposes is the volume of enamel over the entire tooth (Martin, 1983), which if done directly on the specimens necessitates the use of a destructive procedure such as separating the enamel cap from the underlying dentine surface (e.g., Kraus, 1952; Korenhof, 1960; Nager, 1960; Achermann, 1970; Sakai, 1967; Corruccini, 1987a,b). Furthermore, there is no a priori reason to expect that the measurement location by Kay (1981) accurately expresses the average enamel thickness of that particular molar or the thickness of enamel at any other region of that molar crown.

Like Kay (1981), Martin (1983, 1985) developed indices of "average" and "relative" enamel thickness to express the total amount of enamel over a tooth from sections in the plane of the mesial cusps. The index by Martin (1983, 1985) of "relative enamel thickness" is calculated as $[(c/e \times 100)/b^{1/2}]$ where c is the area of the enamel cap, e is the length of the enamel-dentine junction (EDJ), and b is the area of the dentine and pulp enclosed by the EDJ and a line drawn between the buccal and lingual cervical margins. From this dimensionless index, four metric categories of relative enamel thickness were defined: "thin enamel" (mean values of "relative enamel thickness" between 8.90–11.30), "intermediate/thin enamel" (mean values between 11.30–14.65), "intermediate/thick enamel" (mean values between 14.65–17.25), and "thick enamel" (mean values between 17.70–26.20). Together with data on the rate of enamel secretion and prism packing patterns, it was concluded that the common ancestor of the great ape and human clade had thick, fast-forming enamel which was maintained in lineages leading to both orangutans and modern humans. More recent enamel thickness studies focusing on extant hominoids (Beynon et al., 1991) and both prosimians and anthropoids (Shellis et al., 1998), however, concluded that the ancestral condition for the great ape and human clade was thin enamel (or perhaps even average or intermediately thick), and that the thick enamel shared by orangutans and humans evolved in parallel.

Patterning of enamel thickness

Only recently have studies shifted from focusing on the phylogenetic utility of relative enamel thickness to asking sharper questions about the relationship between tooth function and the *distribution* of enamel across the tooth crown, i.e., the patterning of enamel thickness distribution. Enamel is distributed in a complicated manner that corresponds closely to the various functional

demands placed on particular regions of molar crowns, such that "functional" cusps[1] (protocones and protoconids) possess relatively thicker enamel than corresponding "nonfunctional" cusps (paracones and metaconids) (Shillingburg and Grace, 1973; Gantt, 1977; Molnar and Gantt, 1977; Khera et al., 1990; Macho and Berner, 1993, 1994). At a more detailed level, regional loading regimes within a molar can be determined from details of macroscopic wear patterns. The placement of wear facets across a tooth crown provides clues as to which phase of chewing occurs predominantly over a particular region of a cusp (Butler, 1956, 1967; Mills, 1955, 1963; Kay and Hiiemae, 1974a,b; Kay, 1975, 1977, 1978; Grine, 1981). The first phase of the power stroke of chewing, the buccal phase (phase I), occurs when mandibular molars move supero-medially across the maxillary cusps and into centric occlusion, while the second phase, or lingual phase (phase II), occurs when the mandibular cusps move infero-medially across the maxillary cusps and out of centric occlusion (Fig. 1). As a result, two distinct sets of wear facets are produced: phase I facets appear along the lingual slopes of maxillary cusps and the buccal slopes of mandibular cusps, whereas phase II facets appear along the buccal occlusal slope of the protocone and hypocone and the lingual occlusal slope of the protoconid, hypoconid, and hypoconulid (Mills, 1955, 1963) (Fig. 2). Moreover, the movement of molars during the buccal phase, or phase I, corresponds to shearing activity, while phase II mastication is mainly associated with crushing activities. Proportionally thicker enamel at a particular region of the tooth crown may therefore be associated with either enhanced phase I or II activity, which in turn is related to the mechanical properties of food items. The advantage of using the patterning of enamel thickness distribution over estimates of overall enamel thickness is that it allows more refined functional hypotheses to be generated by relating enamel thickness at functionally informative regions of the crown to the biomechanics of the masticatory system. For instance, one series of papers (Macho and Thackeray, 1992; Macho, 1994, 1995; Macho and Berner, 1993, 1994; Spears and Macho, 1995) demonstrated that enamel thickness varies over the molar crown of modern humans in such a way that measures of "average" or "relative" enamel thickness (*sensu* Kay, 1981; Martin, 1983, 1985) may tend to obscure important interspecific differences that are presumably related to patterns of masticatory loading and the functional requirements of various dietary regimes.

Overall, teeth and their supporting structures are subjected to considerable stresses as a result of masticatory loading. The ability of teeth to effectively distribute stress is related not only to the thickness and quality of enamel, but to the topography of the enamel cap and the distribution of stiffness within the materials that comprise the tooth, i.e., enamel and dentine. To remain functionally competent throughout the lifetime of an individual, teeth must be able to distribute stress in a way that minimizes the possibility of crack propagation and failure due to fatigue. Decussation of enamel prisms from their origin along the EDJ to the outer enamel surface reduces the mechanical likelihood of crack propagation (e.g., Pfretzschner, 1986; von Koenigswald et al., 1987). At the same time, prism decussation reduces the efficacy of enamel to dissipate tensile stresses, especially directed perpendicular to the long axis of prism rods. Because enamel is more resistant to stress in one direction than another, it is considered to be anisotropic (Yettram et al., 1976; van Noort et al., 1991; Spears et al., 1993; Spears and Crompton, 1994). Differences in the pattern of prism decussation, which have been documented among hominin species (Beynon and Wood, 1986; Grine and Martin, 1988), can therefore greatly affect the mechanical efficiency of teeth under various loading regimes.

As the microstructural organization of enamel can severely affect the mechanical properties of enamel, it is important to include these factors in biomechanical analyses of stress distribution within a tooth. If

[1]It should be kept in mind that the terms "functional" and "nonfunctional" are used merely for descriptive purposes and imply nothing about the actual function of the different cusps during mastication. In the literature, "functional" and "nonfunctional" cusps have also been referred to as "loading" and "nonloading" cusps, respectively. All cusps are "functional" and are loaded during occlusion; it is just that different parts of cusps are loaded in different ways.

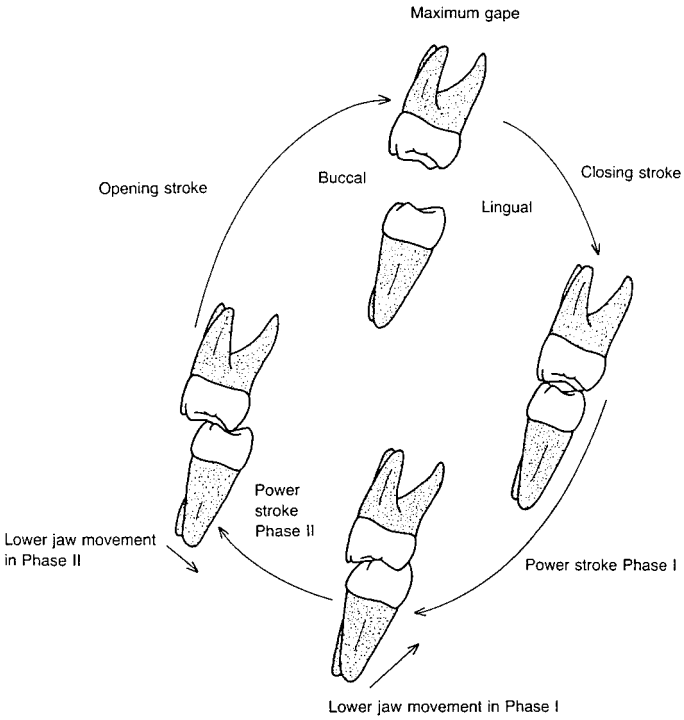

Fig. 1. Schematic illustration of the chewing cycle, detailing the movement of mandibular molars during the closing stroke, the power stroke, and the opening stroke. Phase I of the power stroke occurs when mandibular molars move supero-medially across the maxillary cusps and into centric occlusion, while phase II occurs when the mandibular cusps move infero-medially across the maxillary cusps and out of centric occlusion. The movement of molars during the buccal phase, or phase I, corresponds to the generation of mainly shearing components of the bite force, while phase II mastication is associated with predominantly crushing and grinding activities (reprinted with permission of Simon Hillson and Cambridge University Press).

enamel is modeled as an isotropic structure, the distribution of stress within a tooth induced during mastication is found to flow around the stiff enamel arch into the cervical walls, where it is then transmitted into the roots and underlying alveolus, leaving the dentine core relatively unstressed (Yettram et al., 1976). More recent biomechanical models (e.g., Spears et al., 1993), however, have assumed enamel anisotropy, and incorporated data on the relative stiffness and toughness of enamel and dentine: enamel is very stiff and approximately five times harder than dentine, while dentine is less stiff and nearly four times tougher than enamel (Caldwell et al., 1957; Craig and Peyton, 1958; Rasmussen et al., 1976). From a mechanical perspective, stiffer materials (enamel) perform poorly in the distribution of stress compared to tougher materials (dentine). Modeling enamel as anisotropic results in gradual transmission of masticatory forces across the EDJ into a more compliant dentine core (Spears et al., 1993). The most marked differences between isotropic and anisotropic models is the magnitude of stress incurred in the cervical region; isotropic models produce higher stress levels towards the cervical margin. Lower stresses incurred in the cervical margins would seem to make sense, as these areas possess much less enamel area compared to the remainder of the tooth, rendering them susceptible to enamel fracture and carious lesions (e.g., Lee and Eakle, 1984), and are therefore not optimally designed to dissipate high stress loads.

Other features of molar design also affect the efficacy of redistributing masticatory stresses across teeth. For instance, functional cusps are rounder than nonfunctional cusps (Kraus et al., 1969; Re et al., 1983; Khera et al., 1990). Overall, the characteristically different morphology of functional and nonfunctional cusps affects the potential for abrasion and fracture under masticatory loading, especially during lateral and protrusive masticatory movements (Khera et al., 1990).

Dietary preferences and occlusal morphology

The geometry of the occlusal surface is also known to play a vital role in the process

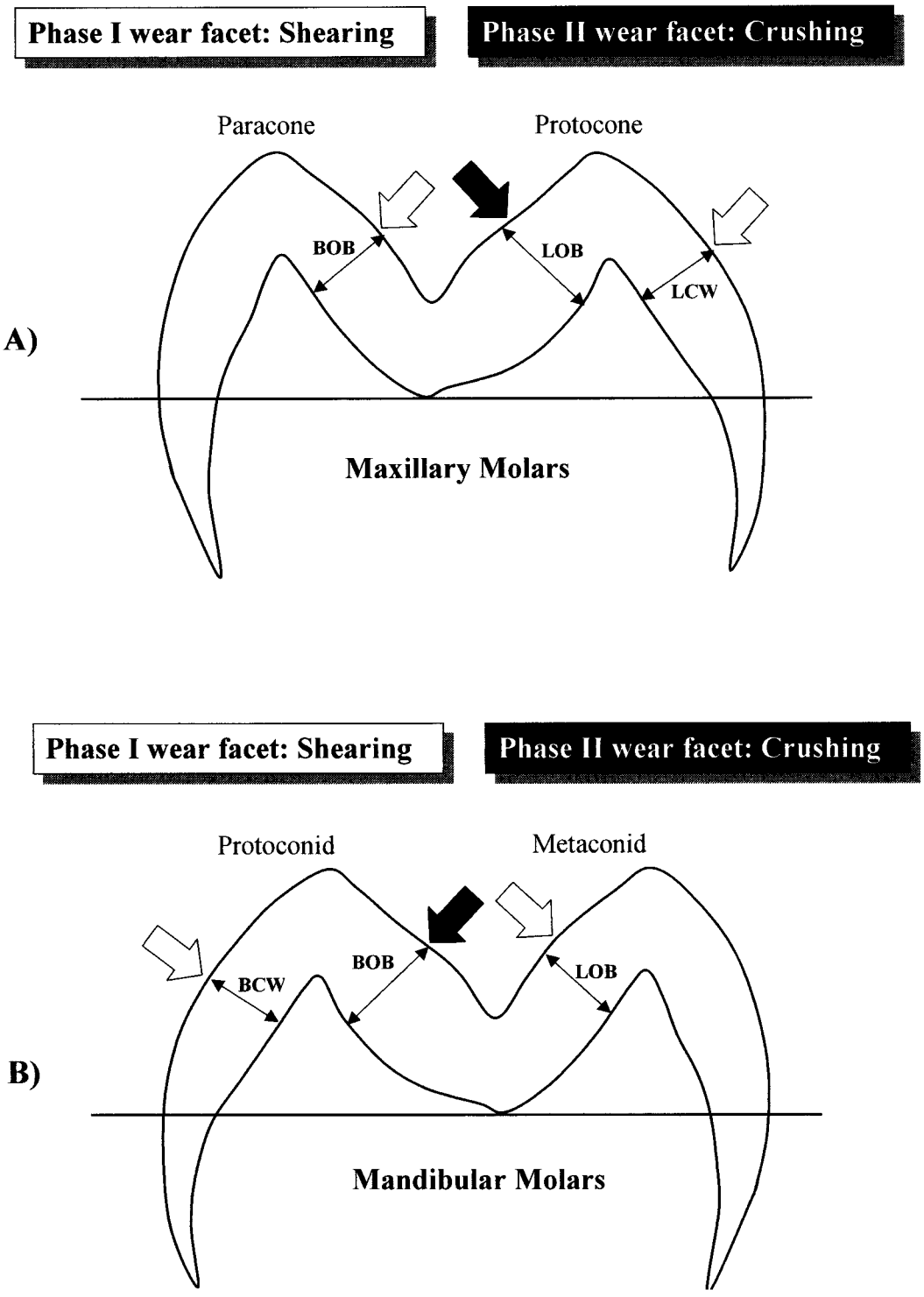

Fig. 2. The two distinct sets of wear facets produced across the mesial cusp region of molars during phase I and II of the power stroke. **A:** Phase I facets (open arrows) appear along the lingual slopes of the paracone and protocone and the buccal slopes of the protoconid and the metaconid. **B:** Phase II facets (solid arrows) appear along the buccal occlusal slope of the protocone and the lingual occlusal slope of the protoconid. BCW, buccal cervical wall; BOB, buccal occlusal basin; LCW, lingual cervical wall; LOB, lingual occlusal basin. Buccal is to the left.

of food reduction. Animals characterized by steep occlusal slopes and high crown relief are adapted towards a more folivorous diet, whereas those species whose molars possess relatively bulbous cusps and more open occlusal basins are able to subsist on a more catholic diet, including a large component of frugivory (e.g., Kay and Hiiemae, 1974; Lumsden and Osborn, 1978; Gordon, 1982; Luke and Lucas, 1983; Hartman, 1988; Spears and Crompton, 1996). Highly-angled cusps and occlusal slopes generate a greater component of surface-parallel loads that are most effective in producing shear stress along the outer enamel surface, whereas low-angled, bulbous cusps and less steep occlusal slopes generate predominantly surface-normal loads that are more effective in producing crushing loads (Kay and Hylander, 1978; Hartman, 1988; Spears and Crompton, 1996). The hominoid taxa included in this study exhibit a wide range of dietary preferences and occlusal morphologies. Field data suggest that *Gorilla* individuals ingest substantial amounts of soft fruits whenever possible, though they are more folivorous than any other hominoid genus included in this analysis; fruit can comprise anywhere from 40–79% of the total food ingested, while leaves, pith, tender shoots, and flowers can make up as much as 60% of the total diet (Sabater Pí, 1977; Tutin and Fernandez, 1985, 1987; Tutin et al., 1991). Resource availability does impact on gorilla diets, such that differences are present between subspecies living in montane vs. lowland tropical forests (Jones and Sabater Pí, 1971; Sabater Pí, 1977; Rogers, 1989; Tutin and Fernandez, 1985, 1987). *Pan* is generally considered a frugivore, though studies conducted in the wild suggest that the habitual consumption of several dozen species of fauna and flora (including birds, bird's eggs, insects, fruits, leaves, leaf buds, seeds, blossoms, stems, pith, bark, and resin) align them more with humans as generalized omnivores (Hladik, 1977; Goodall, 1986; Fleagle, 1988; Tutin et al., 1991). Interestingly, sympatric chimps and gorillas observed within the Lopé Reserve, Central Gabon have similar diets, although gorillas, importantly, consume twice the amount of mature leaves and four times as much pith (Tutin et al., 1991). *Pongo* consumes a variety of hard unripe fruits, leaves, and hard-husked objects such as seeds and bark, along with small amounts of insects, eggs, fungi, and honey (MacKinnon, 1974, 1977; Ungar, 1992; 1995), though *Pongo* can be realiably classed as a frugivore, as fruit forms up to 85% of the total diet (MacKinnon, 1977; Rodman, 1977; Galdikas and Teleki, 1981; Teleki, 1981; Galdikas, 1988). Compared to gorillas, orangutans ingest a higher percentage of fruits with harder, tougher husks (Ungar, 1992, 1995), with bark and wood comprising up to 15% of total food items consumed (Rodman, 1988). All of these ape species have occlusal geometries well-suited to break down the particular food items that comprise the majority of their diets. For instance, molars of *Gorilla* have pointed cusps and steep occlusal slopes which are well-suited to reducing fibrous plant items by shearing activity (Hartman, 1988; Spears and Crompton, 1996). Similarly, *Pongo* subsists on a variety of hard food items which require large amounts of compressive, crushing components of the bite force. Molars of *Pongo* are well-suited to withstand substantial occlusal loads as they possess relatively low, bulbous cusps and shallow occlusal basins (Hartman, 1988; Spears and Crompton, 1996).

Purpose of this study

If the patterning of enamel thickness distribution is at all related to the functional demands of food reduction, then molars of *Pongo* should possess a differential distribution of enamel thickness, reflecting proportionally more crushing components to the bite force. Likewise, molars of *Gorilla* and *Pan* should differ in the distribution of enamel thickness, as these species habitually consume largely different proportions of similar food items.

Aside from its possible relationship to function, the patterning of enamel thickness has been suggested to be a reliable indicator of taxonomic affinity for modern humans, extant hominoids, and early Plio-Pleistocene hominins (Macho and Thackeray, 1992; Macho and Berner, 1993). For this study, the investigation of "taxonomic utility" refers solely to its usefulness in establish-

ing the degree to which this feature can differentiate among extant taxa. This is a necessary exercise, as no study as yet has specifically addressed whether species-specific patterns in the distribution of enamel thickness exist, even though this is crucial to before its application to fossil taxa.

MATERIALS AND METHODS

Since one of the aims of this study is to explore the taxonomic utility of enamel thickness patterning, it is necessary to determine whether or not discrete morphological units can be uncovered in extant species using this feature. To test the hypothesis that species-specific morphologies exist, enamel thickness measurements from a group of extant hominoids are analyzed. The hominoid sample consists of permanent maxillary molars of both male and female *Pongo pygmaeus* (n = 8), *Pan troglodytes* (n = 6) and *Gorilla gorilla* (n = 9), and enamel thickness measurements are taken from scaled photographs of physical cross sections in the plane of the mesial cusps. Unfortunately, it is unknown whether the molars from each taxon represent the same subspecies, though this could be a critical source of variation requiring closer investigation in future comparative studies. The sample of modern humans consists of cross sections taken in the plane of the mesial cusp from 39 unworn maxillary molars ($M^1 = 16$, $M^2 = 12$, $M^3 = 11$) from a Slavic necropolis near Zwentendorf, Lower Austria (10th century A.D.). The modern human sample is the largest to be used in comparative studies of hominoid and hominin enamel thickness, though it is important to point out that resultant measurements of enamel thickness may not be representative of the total range of variation present in contemporary or prehistoric human populations. Future studies should focus on comparisons among populations of *H. sapiens* to determine whether a species-specific pattern of enamel thickness distribution is present.

Measurements

Seven linear measures of enamel thickness were recorded for each cross section across the mesial cusp region (Table 1; Fig. 3). Measurements were recorded to the nearest tenth of a millimeter and were repeated three times (intraobserver errors were below 5% in all cases). All measurements of enamel thickness were taken perpendicular to the EDJ, except for the lingual and buccal cuspal enamel thicknesses, which are measured from the tip of each dentine horn to the tip of the corresponding cusp (see Table 1).

Analytical methods

The analysis of linear or areal measures of enamel thickness in isolation reveals little, as extant hominoids are known to differ markedly in tooth size and as a result, relatively macrodontic species may possess absolutely, but not relatively, thicker enamel. The critical question is whether such differences are functionally equivalent once the effects of size are removed.

Comparisons of morphological differences and similarities among species or groups that differ in body size require that the data are "size-corrected" in one way or another, i.e., the linear covariation of the measurement variable with size is removed. Several options are available for controlling for differences attributable to overall size differences among the taxa under study. Among the most often used techniques are the calculation of ratios or the analysis of residuals from a regression equation. Ratios have been used in many morphometric studies, though their limitations in eliminating size correlations are well-documented (e.g., Atchley et al., 1976; Albrecht, 1978a; Atchley, 1978; Phillips, 1983; Packard and Boardman, 1987, 1988; reviewed in Albrecht et al., 1993). Though it has not yet been applied to studies of enamel thickness, the use of the geometric mean to remove the effects of overall size differences has recently been reviewed (Junger et al., 1995) and may provide a worthwhile avenue of exploration in future studies. Regression analysis, on the other hand, has been the preferred size-adjusting technique in morphometrics, since it reduces size correlations of measurement variables to zero (e.g., Smith, 1984a,b; Albrecht et al., 1993 and references therein).

The application of regression analysis to comparative morphometric studies involves the use of some reference variable as a surrogate of body size; however, the true

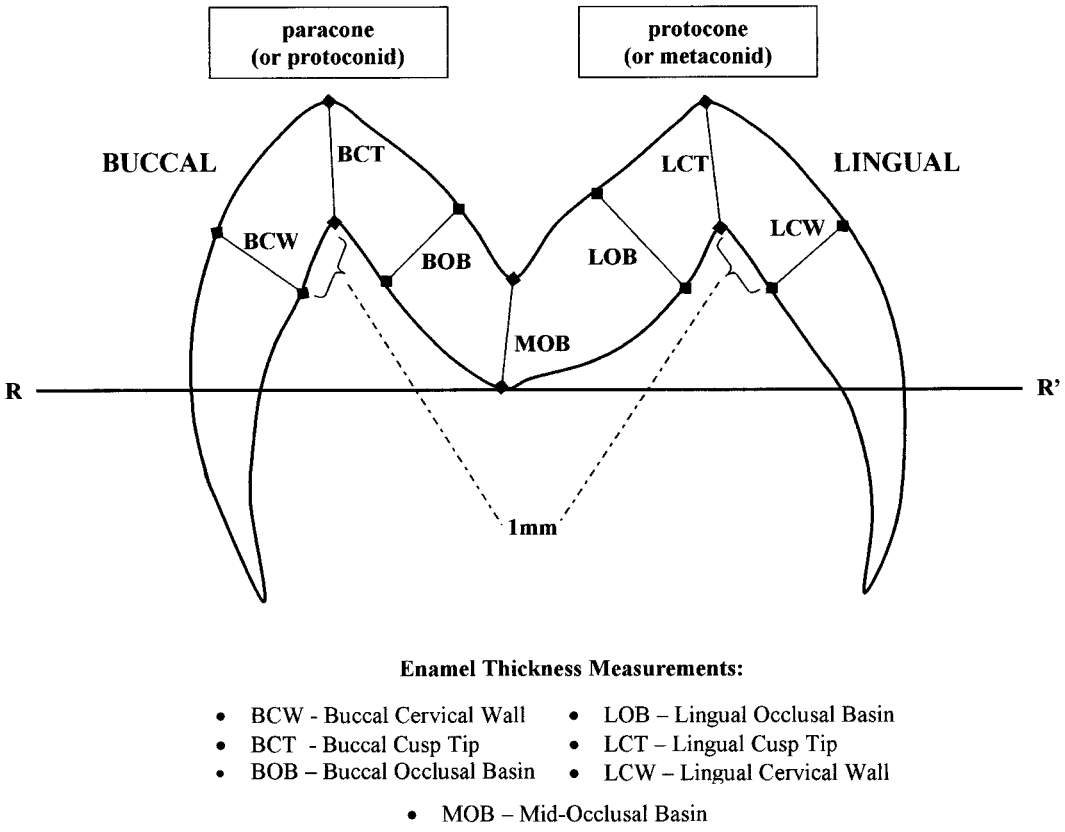

Fig. 3. Schematic diagram of a bucco-lingual cross section through the mesial cusp region of a molar and the location of the seven linear enamel thickness measurements used in this study. All measurements are taken perpendicular to the EDJ; LCW and BCW are recorded 1 mm from the dentine horns (see Schwartz et al., 1998).

scaling relationship of the feature under investigation is obscured if the relationship between body size and the intervening variable is not isometric (Smith, 1981; Hartwig-Sherer and Martin, 1992). The relationship between body size and tooth crown size is considered to be roughly isometric for many primate species (e.g., Kay, 1975; Gingerich et al., 1982), so that the latter is often used as a surrogate for the former in many comparative allometric studies. For primates, it has been demonstrated that enamel thickness is highly positively correlated with the absolute size of the tooth crown (Gantt, 1977; Kay, 1981). Within the past decade or so, several different measures of "tooth crown size" have been used to account for differences in enamel thickness among species. For instance, linear measures of enamel thickness have been scaled against maxillary second molar length to produce a measure of "relative thickness" as a means for making interspecific comparisons (Kay, 1981). Enamel thickness data have also been scaled by dividing each individual thickness measurement by mean crown base area (Beynon and Wood, 1986). More recently, Macho (1994) considered crown areas as a reasonable measure for the scaling of enamel thickness. The observation that discrepancies in crown size and enamel thickness exist between genders of modern humans (females tend to possess smaller teeth endowed with thicker enamel; Alvesalo et al., 1991) cautions against the use of any measure of crown size for scaling purposes. The problem of using crown size measurements for scaling enamel thickness in studies such as this is even more pronounced given that samples are often composed primarily of

TABLE 1. Variables used for analysis of the patterning of enamel thickness distribution[1]

	Measurement (this study)	Prior usage			
		M/G	B/W	G/M	M/T
LCW	Lingual cervical wall. Linear thickness of enamel along the lingual wall of the protocone (or metaconid), 1 mm from dentine horn.	K	LT	LT (L); 1	#3
LCT	Lingual cusp tip. Linear thickness of enamel at the tip of the protocone (or metaconid).	B	CT	CT (L)	#1
LOB	Lingual occlusal basin. Maximum linear thickness of enamel along the buccal face of the protocone (or metaconid).		OT	OT (L); i	#4
MOB	Midocclusal basin. Linear thickness of enamel in the most inferior portion of the occlusal basin.	E		j	#7
BOB	Buccal occlusal basin. Maximum linear thickness of enamel along the lingual face of the paracone (protoconid).		OT	OT (B); h	#5
BCT	Buccal cusp tip. Linear thickness of enamel at the tip of the paracone (or protoconid).	A	CT	CT (B)	#2
BCW	Buccal cervical wall. Linear thickness of enamel along the buccal wall of the paracone (protoconid), 1 mm from dentine horn.	J	LT	LT (B); k	#6

[1] M/G, Gantt (1977) and Molnar and Gantt (1977); B/W, Beynon and Wood (1986); G/M, Martin (1983) and Grine and Martin (1988); M/T, Macho and Thackeray (1992). Maximum lateral enamel thicknesses along the lingual and buccal cervical walls (LCW and BCW, respectively) were recorded approximately 1.0 mm cervical to the dentine horn. This measurement position is preferable over measurements by Martin (1983) of "l" and "k" and "3" and "6" of Macho and Thackeray (1992), where measurements were recorded at the thickest region along the wall of the molar, as the position and size of the Carabelli feature can greatly affect measures of enamel thickness at this particular region of the crown (see Schwartz et al., 1998). LT, lateral thickness; CT, cusp thickness; OT, occlusal thickness.

isolated teeth, where gender allocation is not always possible.

The most often-used scaling factor has been the area of dentine enclosed by the enamel cap (e.g., Martin, 1983; Grine and Martin, 1988; Dumont, 1995). Martin (1983) argued that dentine area, unlike molar length, does not incorporate a component of enamel thickness and is therefore independent from the structure under observation. Although widely used, several problems are associated with using dentine area to eliminate the linear covariation of enamel thickness measurements with overall tooth size. It has been shown that the areas of dentine and enamel exhibit a contrasting pattern of change along the tooth row of modern humans and certain hominin species. Posterior molars possess proportionally more enamel than their anterior counterparts, while the opposite holds true for the amount of dentine (Senyürek, 1939; Zilberman and Smith, 1992; Macho, 1994). This phenomenon is due to different genetic control mechanisms underlying the development of these tissues (e.g., Alvesalo et al., 1991). Regardless, it is unknown whether all components of the tooth crown, i.e., enamel and dentine, are similarly affected by changes in tooth size. Dumont (1995) has shown that the index of "relative enamel thickness" exhibits a weak association with body mass and tooth size, indicating that it does not sufficiently account for variation in enamel thickness due in part to differences in size. Given these problems, it may not be advisable to rely on dentine area as a scaling factor. As a result, it is worthwhile to explore the use of other measurements as a scaling factor.

The dimension of the cervical margin in a bucco-lingual cross section (i.e., the linear distance between the buccal and lingual cemento-enamel junctions) has been suggested as a viable substitute for scaling enamel thickness (Martin, 1983), although the use of this measurement can be problematic due to damages incurred in this region resulting from the process of sectioning. In recent computed tomographic (CT) studies of enamel thickness in hominins, cross-sectional images of the enamel cap were scaled to a standardized length that corresponds very closely to the width of the cervical margin in the scanned plane (Macho and Thackeray, 1992; Macho, 1994; Schwartz et al., 1998).

To eliminate correlations between measurements of enamel thickness and tooth

size, cervical width is used here for several reasons. First, it avoids the problem of correcting for size by using an intervening variable, such as molar length, width, or crown area, which is in part determined by enamel thickness. Second, it allows comparisons with preexisting data sets on modern hominoids that are also scaled to cervical width (e.g., Macho, 1994; Spears and Crompton, 1996). It should also be pointed out that the use of cervical width to "correct for size" among teeth in this study is not an attempt to describe differences in shape.[2]

Cross-sectional images of teeth for all hominoids included in this study are magnified to a standardized cervical width (20 mm). This procedure produces a scaling factor for each image, which is then used to generate size-corrected measurements for interspecific statistical comparisons. As a result, measurements of enamel thickness reported in the figures are presented in arbitrary units. Analyses of the resultant "scaled" measurements are equivalent to adjusting for differences related to the overall size of the tooth by analyzing residuals from regressions of linear enamel thickness measurements onto cervical width. Residuals from a regression equation represent the part of the dependent (= measurement) variable (Y) that is not explained by body size (X), or some surrogate thereof. The scaling factor by which each linear measurement is magnified is directly related and comparable to the proportion of the dependent variable not accounted for by differences in overall size, thereby eliminating the need for analyzing residuals from a regression equation. One particular problem with scaling enamel thickness measurements to cervical width is that results are sample-dependent, as in all residual analyses.

Multivariate procedures, such as discriminant functions analysis (DFA), are useful for quantifying variation in size and shape in biological data (Sneath and Sokal, 1973; Reyment, 1991). This multivariate technique emphasizes the differences among previously determined groupings (i.e., extant species), providing Mahalanobis distances and classification functions to assist judgment of group distinctiveness (Groves, 1970; Howells, 1973; Albrecht, 1978b; Bilsborough and Wood, 1988; Albrecht and Miller, 1993; Shea et al., 1993). Several assumptions about the nature of the data are also implicit in DFA. For instance, it requires that the data follow multivariate normal distributions, though successful discrimination of species may be possible even if this assumption is violated (Manly, 1986). The effective discrimination of taxonomic groupings can also be influenced by inequalities of sample size. Thus, prior probabilities from the DFA are weighted by the number of specimens comprising each sample. Principal components analysis, rather than DFA, has been used in prior investigations of enamel thickness (e.g., Macho and Thackeray, 1992). However, one specific goal of this study is to determine the taxonomic usefulness of enamel cap morphology for discriminating among extant large-bodied hominoids, so that DFA is more appropriate.

The multivariate statistical procedure used here reduces the overall variability into a series of taxonomically informative traits. As a result, DFA aids in clarifying the range of variation in enamel cap structure present in extant hominoids by delineating groups of individual specimens and testing the legitimacy of these groups. The taxonomic usefulness of enamel thickness patterning can then be tested by analyzing the post hoc classifications (generated from the DFA based on equations utilizing the same sample of hominoid molars) for each specimen. The establishment of species-specific morphological patterns in enamel cap morphology in this way will provide a morphological framework within which the most likely taxonomic and functional affinities of early hominin molars can be ascertained.

RESULTS

Though a few studies have commented on the tendency for enamel thickness to increase distally in extant hominoids and/or hominins (e.g., Beynon and Wood, 1986;

[2]Cervical width is also used, as one aim of this study is to provide a comparative basis for interpreting the patterning of enamel thickness distribution in early South African hominins. Data on enamel thickness for the fossil hominins are derived from high-resolution CT scans, where it is difficult to provide accurate and reliable measures of dentine area (see Schwartz et al., 1998 for discussion).

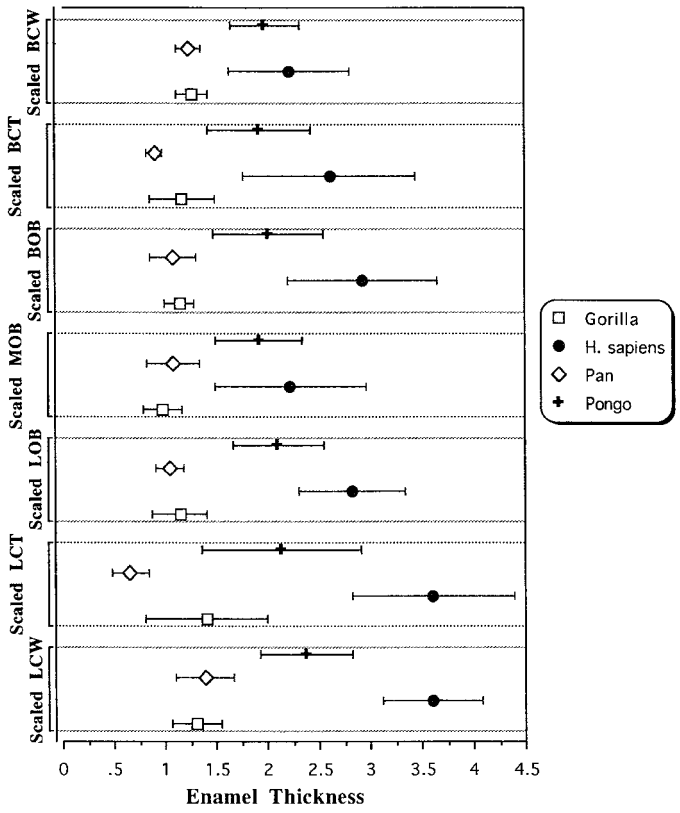

Fig. 4. Comparison of scaled enamel thicknesses for all extant hominoid species in the analysis. Symbols indicate mean values; horizontal lines represent one standard deviation on either side of the mean.

Grine and Martin, 1988; Zilberman and Smith, 1992), most authors have been unable to reliably comment on the presence of such a gradient due to small sample sizes. Recent work by Macho and Berner (1993) demonstrates a systematic difference in the distribution of enamel thickness within the maxillary molar series of *Homo sapiens.* However, sample sizes of other extant large-bodied hominoids remain too small to allow meaningful statistical comparisons among molar types. As a result, multivariate statistical analyses are performed on pooled samples of molar categories. Summary statistics of scaled enamel thickness values at each region of the molar crown for extant hominoid maxillary molars are listed in Table 2, and a comparison of mean enamel thickness values at each region of the crown is shown for each species in Table 3 and in Figure 4. For all statistical comparisons among species, scaled or relative enamel thicknesses (sensu stricto) are used, as the included hominoid taxa differ markedly from one another in body size and dental metrics.

Variation in enamel thickness

The range of variation in relative enamel thickness in both of the thick-enameled hominoids, *Pongo* and *Homo,* is relatively large compared to *Pan* and *Gorilla* at all seven regions of maxillary molar crowns. *Pongo* and *Homo* overlap with one another for all measurements, while the degree of overlap with the thin-enameled hominoids is minimal, except along the lingual part of the protocone (lingual crisp tip, LCT; lingual cervical wall, LCW) (Table 2; Fig. 4). Relative enamel thickness values for the African apes are significantly less than for *Pongo* and *Homo* at all locations across the tooth crown, except at the protocone tip (LCT) for *Gorilla* relative to *Pongo* (Table 3). Mean values for *Pan* and *Gorilla* molars are nearly coincident except at the protocone tip (LCT), and do not differ significantly from one

TABLE 2. Descriptive statistics for the seven scaled linear measurements of molar enamel thickness (in mm) for each extant hominoid taxa (all molar positions combined)

	N	Mean	SD	SE	Observed range
Lingual cervical wall (LCW)					
Pan	6	1.39	0.29	0.12	0.92–1.82
Gorilla	9	1.32	0.24	0.08	0.98–1.63
Pongo	8	2.38	0.44	0.16	1.89–3.05
Homo	39	3.58	0.52	0.08	2.36–4.83
Lingual cusp tip (LCT)					
Pan	6	0.66	0.18	0.07	0.46–0.98
Gorilla	9	1.41	0.59	0.20	0.56–2.35
Pongo	8	2.14	0.78	0.28	1.15–3.61
Homo	37	3.60	0.76	0.12	2.13–5.01
Lingual occlusal basin (LOB)					
Pan	6	1.05	0.14	0.06	0.86–1.28
Gorilla	9	1.15	0.26	0.09	0.80–1.63
Pongo	8	2.11	0.43	0.15	1.59–2.90
Homo	39	2.84	0.53	0.08	1.73–3.95
Midocclusal basin (MOB)					
Pan	6	1.08	0.26	0.11	0.65–1.34
Gorilla	9	0.98	0.19	0.06	0.70–1.33
Pongo	8	1.93	0.42	0.15	1.33–2.58
Homo	39	2.32	0.74	0.11	0.59–3.81
Buccal occlusal basin (BOB)					
Pan	6	1.09	0.23	0.09	0.77–1.35
Gorilla	9	1.15	0.15	0.05	0.88–1.33
Pongo	8	2.02	0.53	0.19	1.40–3.12
Homo	39	2.91	0.71	0.11	1.82–4.62
Buccal cusp tip (BCT)					
Pan	6	0.91	0.08	0.03	0.79–0.98
Gorilla	9	1.18	0.32	0.11	0.53–1.61
Pongo	8	1.93	0.49	0.17	1.38–2.90
Homo	37	2.64	0.80	0.13	0.69–4.12
Buccal cervical wall (BCW)					
Pan	6	1.24	0.12	0.05	1.09–1.38
Gorilla	9	1.28	0.15	0.05	1.00–1.49
Pongo	8	1.99	0.33	0.12	1.59–2.55
Homo	39	2.25	0.57	0.09	1.13–2.23

another at most locations across the molar crown. Conversely, *Homo* possesses significantly thicker enamel than *Pongo* at most places across the molar crown except at the midocclusal basin (MOB) and buccal cervical wall (BCW) (Table 3). These similarities and differences seem to indicate a more complicated pattern of enamel thickness distribution than is recognizable by comparing indices of "relative" or "average" enamel thickness (sensu Martin, 1983; Grine and Martin, 1988; Dumont, 1995). As a result, a comparative dichotomy of "thin-enameled" and "thick-enameled" based on such indices or at one particular region of the crown (e.g., Kay, 1981; Beynon and Wood, 1986; Conroy, 1991) may underestimate proportional differences in enamel thickness in teeth of hominoid taxa, which may prove critical in investigating the taxonomic, functional, and phylogenetic importance of enamel thickness patterning.

Patterning of enamel thickness distribution

A distribution profile displaying mean values of enamel thickness at each of the measurement locations for the pooled sample of maxillary molars for each extant hominoid species is shown in Figure 5 (the numerical scale is arbitrary, as each cross-sectional image of the enamel cap is scaled to a standardized cervical width). All of the hominoids except *Homo* exhibit relatively little change in the distribution of enamel across the mesial portion of the molar crown (Fig. 5). *Pan* and *Pongo* maxillary molars are characterized by relatively thinner enamel at both the lingual and buccal cusp tips compared to the cervical walls. Overall, *Pongo* maxillary molars possess intermediately thick enamel, but like the African apes, show only minor changes in the distribution of enamel thickness across the tooth crown. *Homo sapiens* molars, on the other hand, display marked variation in enamel thickness across the mesial cusp region, with the protocone being endowed with thicker enamel relative to the paracone. On average, *Homo* molars also display thicker enamel along the occlusal aspect of the protocone (buccal occlusal basin, (BOB) relative to the buccal portion of the paracone (buccal cuspal tip, BCT; buccal cervical wall, BCW), a condition not seen in any other hominoid. This results in a sharp decrease in enamel thickness extending from the buccal portion of the occlusal basin to the buccal portion of the paracone, i.e., from BOB to BCW, in *Homo* as compared to a slight increase in enamel thickness in these regions of the crown in the other hominoid taxa.

Several studies have drawn attention to the distribution of enamel thickness within the context of occlusal loading regimes (e.g., Shillingburg and Grace, 1973; Gantt, 1977; Molnar and Gantt, 1977; Martin, 1983; Grine

TABLE 3. Statistical comparison (Mann-Whitney U test) of scaled enamel thickness values (in mm) for each pair of extant hominoid taxa[1]

		Pan		*Gorilla*		*Pongo*	
	Mean	U	*P*	U	*P*	U	*P*
Lingual cervical wall (LCW)							
Pan	1.39						
Gorilla	1.32	21	NS				
Pongo	2.38	0	<0.005	0	<0.001		
Homo	3.58	0	<0.001	0	<0.001	10	<0.001
Lingual cusp tip (LCT)							
Pan	0.66						
Gorilla	1.41	5	<0.010				
Pongo	2.14	0	<0.005	16	NS		
Homo	3.60	0	<0.001	5	<0.001	32	<0.001
Lingual occlusal basin (LOB)							
Pan	1.05						
Gorilla	1.15	21	NS				
Pongo	2.11	0	<0.005	1	<0.001		
Homo	2.84	0	<0.001	0	<0.001	47	<0.005
Midocclusal basin (MOB)							
Pan	1.08						
Gorilla	0.98	10	NS				
Pongo	1.93	1	<0.005	1	<0.001		
Homo	2.32	19	<0.001	24	<0.001	105	NS
Buccal occlusal basin (BOB)							
Pan	1.09						
Gorilla	1.15	23	NS				
Pongo	2.02	0	<0.005	0	<0.001		
Homo	2.91	0	<0.001	0	<0.001	45	<0.005
Buccal cusp tip (BCT)							
Pan	0.91						
Gorilla	1.18	11	NS				
Pongo	1.93	0	<0.005	2	<0.005		
Homo	2.64	6	<0.001	15	<0.001	75	<0.050
Buccal cervical wall (BCW)							
Pan	1.24						
Gorilla	1.28	23	NS				
Pongo	1.99	0	<0.005	0	<0.001		
Homo	2.25	12	<0.001	27	<0.001	116	NS

[1] NS, not significant.

and Martin, 1988; Macho and Thackeray, 1992). The distribution profiles presented here lend partial support to the hypothesis that "loading" areas of the crown have thicker enamel than "nonloading" areas, i.e., maxillary lingual cusps possess thicker enamel than their buccal counterparts. This is most apparent in the molars of *H. sapiens* and *Pongo* but less so in the African apes. Surprisingly, *Pan* maxillary molars possess thinner enamel on average across the protocone tip (LCT) than at the paracone tip (BCT) (see Fig. 5). Wilcoxon signed rank tests are used to test for differences between corresponding "functional" and "nonfunctional" regions of the crown, the results of which are listed in Table 4. Functional cusps are endowed with significantly more enamel in *H. sapiens* along the cervical slopes (LCW vs. BCW) and cusp tips (LCT vs. BCT). Compared to modern humans, extant apes tend to be characterized by less marked differences between functional and nonfunctional regions of cusps, though *Pongo* molars are characterized by thicker enamel along the lingual cervical wall. Sample sizes are small for each species, such that statistical tests have low power. In particular, it would be important to test for differences between "loading" and "nonloading" cusps within each tooth category for both maxillary and mandibular molars. As samples for each great ape species rarely reach above 2–3 molars for each category, it is not advisable to test functional hypotheses of enamel thickness distribution within molar types until larger samples of teeth become available for analysis. With this caveat in mind, it is still important to examine trends in the pattern of differences, as they are important in light

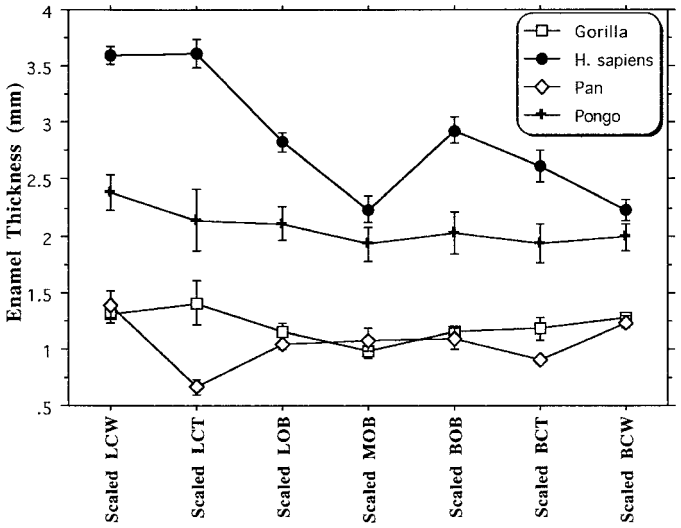

Fig. 5. Distribution profile of scaled enamel thickness measurements across the maxillary molar crown in extant hominoids. Symbols indicate mean values; vertical bars represent one standard error on either side of the mean.

TABLE 4. Results of paired statistical comparisons (Wilcoxon signed rank tests, P *values) between corresponding enamel thickness measurements on the lingual and buccal aspects of molars for each hominoid taxon*[1]

	Paired tests		
	LCW/BCW	LCT/BCT	LOB/BOB
Pan	0.345	0.046	0.345
Gorilla	0.767	0.249	0.813
Pongo	0.008	0.097	0.093
Homo	<0.001	<0.001	0.379

[1] LCW, lingual cervical wall; BCW, buccal cervical wall; LCT, lingual cusp tip; BCT, buccal cusp tip; LOB, lingual occlusal basin; BOB, buccal occlusal basin.

TABLE 5. Predicted group membership from DFA on relative (i.e., scaled) enamel thickness values in extant hominoid maxillary molars

		Predicted group membership[1]			
Species	N	*Pan*	*Gorilla*	*Pongo*	*Homo*
Pan	6	5 (83.3%)	1 (16.7%)	0 (0%)	0 (0%)
Gorilla	9	3 (33.3%)	6 (66.7%)	0 (0%)	0 (0%)
Pongo	8	0 (0%)	0 (0%)	6 (75.0%)	2 (25.0%)
Homo	37	0 (0%)	0 (0%)	0 (0%)	37 (100.0%)

[1] Percentages of molar specimens assigned to each hominoid species are provided in parentheses; 90.0% of all individual molar specimens are correctly reclassified.

of the proposed functional significance of enamel thickness patterning within teeth.

Taxonomic utility of enamel thickness patterning

To determine the efficacy of enamel thickness patterning in discriminating among fossil hominin taxa, it is imperative to examine the extent to which this feature describes the variation in enamel thickness across the tooth crown in known taxa. Thus, DFA is used to investigate differences in enamel thickness patterning (using scaled enamel thickness measurements) among maxillary molars of extant hominoids.

The distribution of enamel thickness reclassifies extant hominoid maxillary molar specimens with 90% accuracy: 100% of modern human, 75.0% of *Pongo,* 83.3% of *Pan,* and 66.6% of *Gorilla* are correctly reclassified. One *Pan* molar and three *Gorilla* molars are incorrectly placed into *Gorilla* and *Pan,* respectively, while 2 of the 8 *Pongo* molars are grouped with *Homo,* indicating that the distribution of enamel thickness reliably distinguishes between thick-enameled and thin-enameled hominoid molars (Table 5).

Standardized discriminant function coefficients, eigenvalues, and percentage contribution of each function to the overall variance for DFA of enamel thickness patterning in maxillary molars are listed in Table 6. The first discriminant function is statistically significant ($P < 0.05$; Wilks-Lambda) and separates modern humans from the remaining hominoid taxa. Discrimination along this axis is due to proportionally thicker enamel along the lingual slope of the protocone (LCW) and buccal slope of the paracone (BOB), on the one hand, and on the other, thinner enamel at the tip of the paracone

TABLE 6. First two standardized discriminant functions based on an analysis of enamel thickness distribution in extant hominoid maxillary molars[1]

Variables	DF1	DF2
LCW	1.32 (0.94)	−0.96 (0.08)
LCT	0.00 (0.65)	1.86 (0.62)
LOB	−0.11 (0.69)	−0.16 (0.15)
MOB	0.05 (0.34)	−0.15 (−0.11)
BOB	0.12 (0.55)	−0.37 (0.13)
BCT	−0.48 (0.40)	−0.12 (0.22)
BCW	−0.18 (0.34)	0.33 (0.00)
Wilks-Lambda	0.03	0.09
Eigenvalues	5.63	0.27
% variance	92.24	4.52

[1] LCW, lingual cervical wall; LCT, lingual cusp tip; LOB, lingual occlusal basin; MOB, midocclusal basin; BOB, buccal occlusal basin; BCT, buccal cusp tip; BCW, buccal cervical wall. *P*-values from Wilks-Lambda tests are also provided. Listed for each variable are the standardized discriminant function coefficients, eigenvalues, and percentage of variance.
Pooled within-group correlations between each variable and the discriminant function are listed in parentheses.

(BCT), lingual slope of the protocone (LOB), and paracone wall (BCW) (Table 6; Fig. 6), i.e., modern humans have high positive factor scores for LCW and BOB along this axis, while the remaining hominoid species have negative scores. The major difference in enamel cap structure between modern human and extant ape maxillary molars occurs between areas of the crown corresponding to phase I wear facets (LCW and BOB) and phase II wear facets (LOB), and therefore indicates a structural adaptation towards proportionally more shearing activity than crushing/grinding activity in modern human molars. Though molars of *H. sapiens* and *P. pygmaeus* have traditionally been considered to be "thick-enameled" (e.g., Gantt, 1977; Martin, 1983), results suggest that these hominoid species differ in their proportional distribution of enamel thickness in a way that is related to the functional demands of different dietary repertoires.

The second discriminant function is not statistically significant ($P = 0.09$, Wilks-Lambda), most likely due to the marked variation along this axis for both *Homo* and *Pongo* molars, though it tends to separate *Pan* maxillary molars from the majority of *Gorilla* molars (see Fig. 6): two thirds of all *Gorilla* molars have positive scores along this axis, while all molars of *Pan* have negative scores. Discrimination along this axis is due to proportionally thicker enamel at the protocone tip (LCT) and paracone wall (BCW) compared to that at all other regions of the tooth crown (Table 6). The presence of proportionally thicker enamel across the majority of the crown surface in *Pan* compared to *Gorilla* may be indicative of the ability of chimpanzee molars to induce relatively greater compressive forces during occlusion. In a biomechanical appraisal of occlusal morphology, Spears and Crompton (1996) found the molars of *Gorilla* able to induce greater shear stress compared to *Pan* molars. The results presented here therefore provide additional evidence that the enamel caps of *Gorilla* and *Pan* are structurally dissimilar, and that this is likely a direct reflection of differences in dietary preferences and the proportions of similar food items in the diet. This is especially important, as both species have historically been considered to belong to a morphologically homogeneous "thin-enameled" group (Martin, 1983; Grine and Martin, 1988).

DISCUSSION

At present, it is not possible to comment realiably on whether enamel thickness, or some measure of the overall amount of enamel, changes from anterior to posterior in hominins, as sample sizes of extant large-bodied apes remain too small to allow meaningful comparisons among molar types. However, recent studies on modern humans indicate that not only is enamel distributed within a tooth in a predictable manner, but that posterior molars have thicker enamel compared to their anterior counterparts (Macho and Berner, 1993, 1994; Spears and Macho, 1995). This anterior-posterior gradient in enamel thickness is most likely related to the occurrence of increased occlusal loading forces in the posterior molars, thereby affording them with greater functional durability (Mansour and Reynick, 1975; Molnar and Ward, 1977; Ward and Molnar, 1980; Osborn and Baragar, 1985; Koolstra et al., 1988; Janis and Fortelius, 1988). Higher crush to shear ratios (i.e., bite forces) have been documented in the posterior molar region of humans and are due, at least in part, to the anterior tilt of teeth resulting from an accentuated curve of Spee (Osborn, 1993).

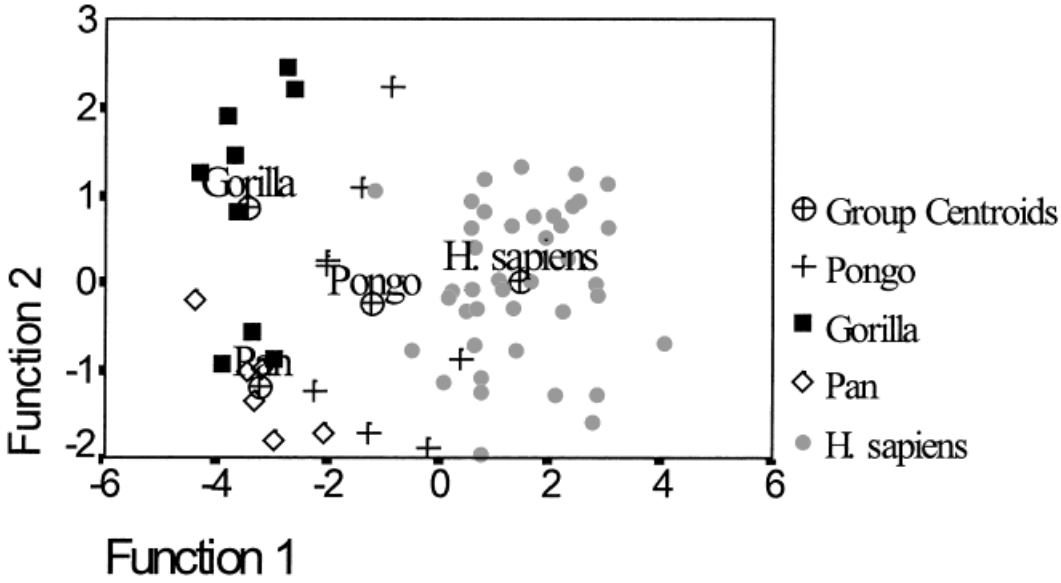

Fig. 6. Plot of the first two canonical discriminant functions, based on an analysis of all seven scaled linear enamel thickness measurements, showing the position of each hominoid specimen and the group centroids.

Gradient-related changes in enamel thickness along the molar series of modern humans have also been interpreted as evidence for a disparity in masticatory loads between functional (protocone) and nonfunctional (paracone) cusps (Spears and Macho, 1995). A tendency towards increased "symmetry" in enamel thickness overlying corresponding functional and nonfunctional portions of the crown can be interpreted as an indication of more equivalent occlusal forces exerted over the protocone and paracone. Conversely, increasing "asymmetry" in enamel thickness between corresponding functional and nonfunctional regions of the molar may indicate a more strict reliance on either shearing or crushing/grinding as the predominant masticatory stress regime. The finding of increasing "symmetry" in modern human molars led Spears and Macho (1995) to the conclusion that masticatory loads exerted over the protocone and paracone become more equal in the posterior molars: "The distinction between functional and nonfunctional cusps [in the posterior molars] is less clear than it is in first maxillary molars where the protocone is clearly more prominent" (Spears and Macho, 1995, p 395). This suggested to them the presence of a functional gradient in modern humans whereby anterior molars perform more shearing, and posterior molars perform more crushing and grinding. This pattern has also been observed in certain extant apes. Based on an analysis of microwear features and occlusal facet orientation, Gordon (1982, 1984) found that posterior molars of *Pan* are characterized by greater crush/shear ratios (pit frequencies on crushing surfaces range from 30% in first molars to over 50% in third molars) and flatter facet orientation, indicating that greater compressive forces are incurred in the posterior molar region. This fact may help explain why *Pan* molars seem to fall out as structurally dissimilar compared to those of *Gorilla,* based on the patterning of enamel thickness (see Table 5; Fig. 6).

The results presented here indicate a direct link between the patterning of enamel thickness distribution, tooth function, and dietary proclivities. Further complicating matters is the possibility that sex chromosomes and/or sex hormones influence enamel thickness, although this has not been thoroughly tested. Studies on modern humans

(Moss and Moss-Salentjin, 1976; Moss, 1978) attributed differences in enamel thickness between sexes to extensions in the duration of amelogenesis, while the secretory rate remained the same. Many clinical studies on modern humans support the notion of sexual differences in enamel thickness, though whether or not this is a feature common to all nonhuman primates has not been adequately established (see Macho, 1995 and references therein). Understanding the variation in enamel thickness due to sexual dimorphism is especially problematic in studies of isolated extant and fossil teeth; unfortunately, "teeth do not bear recognizable gonads" (Oxnard, 1987, p 65), so that it is virtually impossible to separate them by sex. Future studies should focus specifically on differences in enamel thickness, and its distribution across the tooth crown, between sexes of modern humans and extant great apes, and to try to integrate such data with information on possible sex differences in aspects of enamel development (e.g., Schwartz and Dean, 1999).

The differences found here among extant large-bodied hominoids suggest that studies focusing on overall measures of "enamel thickness" obscure the strong functional signal of localized increases or decreases in enamel thickness at functionally relevant regions of the tooth crown. As such, estimates of enamel area or enamel volume may be better suited to phylogenetic interpretations, though it is important to bear in mind that morphological features must be shown to be developmentally homologous across all included taxa before submission to any phylogenetic analysis. The total amount of enamel, usually estimated as the area of enamel in an exposed section scaled to some measure of tooth size, has figured prominently in many phylogenetic analyses of hominoid evolution. It has also been recognized for some time that aspects of tooth crown development should be included in such analyses (e.g., Martin, 1983, 1985; Grine and Martin, 1988; Beynon et al., 1991, 1998; Schwartz and Dean, 1998; Shellis et al., 1999).

Information from incremental markings, especially the rate of enamel secretion, has been used to generate hypotheses regarding the developmental mechanisms for thin and thick enamel. Martin (1983, 1985) suggested that differences in enamel thickness among hominoids can be accounted for by varying secretion rates within different portions of the developing tooth crown. For example, he proposed that thin-enameled species such as the African apes were characterized by a reduction in the daily secretion rate in the outer enamel, although little quantitative data on daily enamel secretion rates were presented as evidence of this fact. Using the thickness and rate of enamel development, he postulated a thick-enameled ancestor for the great ape and human clade, with thin enamel being the primitive condition for all hominoids (Fig. 7). It is now accepted, however, that differences in daily enamel secretion rates between regions of the same tooth are greater than those between species, so that the comparative dichotomy of "slow-forming" vs. "fast-forming" enamel has little taxonomic utility. Beynon et al. (1991) undertook a more detailed study of secretion rates to directly test whether there is a developmental slowing of enamel formation in the outer enamel of African apes. Their results indicated little evidence for a developmental slowing in secretory *rates,* as Martin (1983) had suggested, but rather a reduction in the secretory *period* of ameloblasts during crown formation, and that it was this reduced developmental period which accounts for the thin enamel in African apes. They then concluded that the ancestral condition for the great ape and human clade was thin enamel, and that the thick enamel shared in lineages leading to orangutans and humans evolved in parallel (Fig. 7). More recently, Shellis et al. (1998) argued that compared to extant anthropoids, most hominoids seem to possess enamel of average thickness/thinness, with two notable exceptions: modern humans exhibit relatively thick and gorillas exhibit relatively thin enamel for anthropoids of their body mass (Fig. 7).

Whatever the plesiomorphic condition may be for hominoids, it is entirely possible that a very simple developmental mechanism can be invoked to explain the sometimes subtle differences in the achievement of adult morphology. For instance, human and

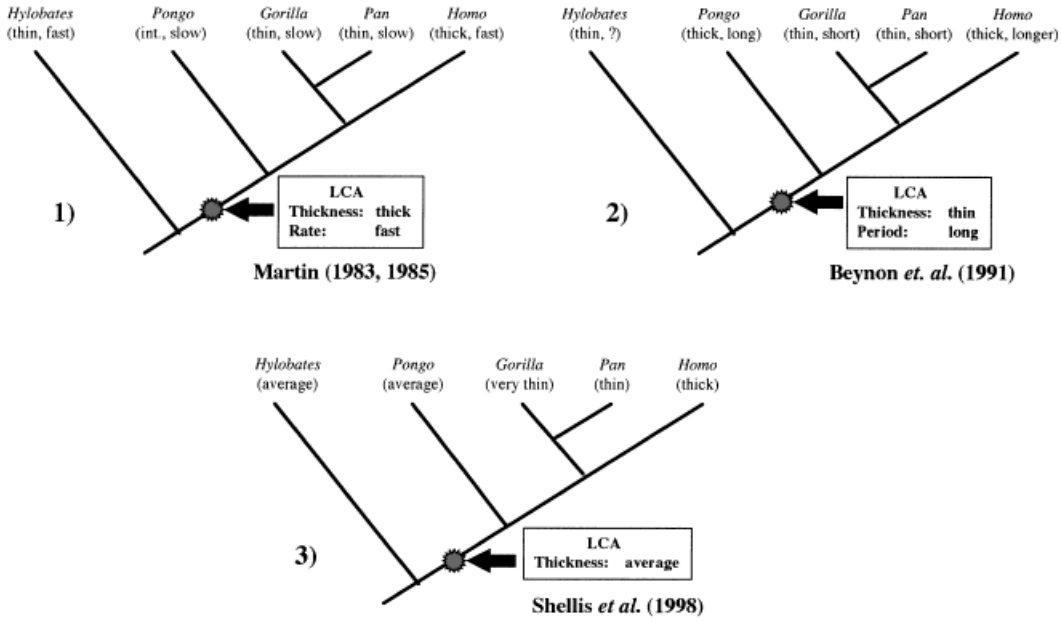

Fig. 7. Cladograms depicting various phylogenetic scenarios for the evolution of thick enamel within the great ape and human clade, as well as information on relative enamel thickness, rate of deposition, and the relative period of formation for each taxon, as well as the character states for the purported last common ancestor (LCA). **1:** Based on Martin (1983, 1985), who proposed that the Asian and African great apes had intermediately thick (*Pongo*) and thin (*Pan, Gorilla*) enamel that formed at a relatively slow rate of secretion. Hylobatids and *Homo* both have enamel that formed relatively quickly, though the former has relatively thin enamel and the latter has much thicker enamel. Based on outgroup analysis, the LCA of great apes and humans was seen to possess thick enamel that formed at a relatively fast rate. **2:** Beynon et al. (1991) suggested that it was not the rate of enamel formation which differed but the period over which it was secreted. Thus, according to them, the LCA of great apes and humans possessed relatively thin enamel that formed over a relatively longer time. **3:** Recent work by Shellis et al. (1998) showed that relative to body/tooth size, *Hylobates* and *Pongo* have "averagely" thick enamel, while the African apes are relatively thin-enameled. *Homo,* on the other hand, has relatively thick enamel for an anthropoid of its body mass.

orangutan molars possess a reasonably similar degree of enamel thickness, and the possibility exists that despite similarities in morphology, each species follows a different sequence of secretory activity of enamel to achieve the final, albeit similar, degree of enamel thickness. Such a finding would suggest that the shared possession of "thick" or "thin" enamel among species is phylogentically uninformative, as it would not represent a developmental synapomorphy. Different regions of teeth form at different rates, and over different periods, resulting in varying degrees of enamel thickness across the tooth crown. Therefore, it would be desirable to document the pattern of enamel developmental at all regions of the crown in all hominoid species, in order to build up a developmental profile for teeth belonging to each species. Though this is quite a monumental task, it has been at least possible to compare the time and rate of enamel development across just one region of the crown, the cusp tip, in extant large-bodied hominoids using incremental markings, most notably the daily cross striations easily visible as fine dark lines that run transversely across the long axis of enamel prisms[3] (see Schwartz and Dean, 1999). Results from that study suggest that the control of enamel secretion at a cellular level in the cuspal regions of hominoid teeth may be different

[3]Cross striations reflect the circadian secretory activity of ameloblasts and are crucial to studies of crown initiation, formation, and completion times from histological studies (Reid et al., 1998 and references therein). Sometimes cross striations may correspond in position to regular varicositics or constrictions along the length of prisms, which are best seen in scanning electron microscopy.

between one species and another and even from tooth type to tooth type. It may even vary from one cusp to another in the same tooth. Most importantly, this kind of approach may help reveal developmental mechanisms that determine different thicknesses of cuspal enamel in primate teeth in a way that linear and areal measurements of enamel thickness cannot. Ontogenetic information such as this can provide some insight into the way not only cuspal enamel, but the entire enamel cap, has come to be thick or thin throughout primate evolution. Moreover, the apparent disparity in cusp tip development among extant hominoids underscores the importance of including developmental information in phylogenetic analyses of enamel thickness. It is entirely possible, however, that such differences occur in the cusp tip only, or perhaps only in posterior teeth, so that other regions of extant and extinct hominoid tooth crowns need to be examined to establish the precise phylogenetic valence of enamel thickness and development throughout hominoid evolution.

CONCLUSIONS

The timing and pattern of tooth morphogenesis are broadly similar among hominoids, while differences in enamel thickness are marked. Generally speaking, the amount of enamel across the tooth crown is related to particular dietary regimes, such that animals with thick enamel subsist on a diet of hard food items, while those with thin enamel are more folivorous. Enamel is distributed across a tooth in a complicated manner that corresponds closely to the various functional demands placed on particular regions of the crown, such that functional cusps (maxillary lingual cusps and mandibular buccal cusps) possess relatively thicker enamel than corresponding nonfunctional cusps (maxillary buccal cusps and mandibular lingual cusps). The distribution, or patterning, of enamel thickness allows more refined functional hypotheses to be generated by relating enamel thickness at functionally informative regions (i.e., phase I vs. phase II facets) of the crown to the biomechanics of the masticatory system. Though the patterning of enamel thickness distribution needs to be investigated in larger samples of hominoid maxillary and mandibular molars, the high prediction rates in all hominoid taxa suggest that this feature possesses a strong taxonomic signal, i.e., similarities at this level allow the sorting of individuals into phena that closely correspond to the extant species of great apes. These results are important, as most earlier studies on hominoid enamel thickness lumped the African apes into a "thin-enameled" category and *Pongo* and *Homo* into a "thick-enameled" category. It would seem that at a more refined functional level, this comparative dichotomy is no longer tenable, as differences in the patterning of enamel thickness are evident within each category: (1) *Pan* maxillary molars are structurally dissimilar from those of *Gorilla* in the possession of proportionally thinner enamel at the protocone tip (LCT) compared to all other regions of the tooth crown; and (2) extant *Homo* maxillary molars are distinct from those of *Pongo* in that the former are characterized by proportionally thicker enamel at the lingual slopes of the paracone (BOB) and protocone (LCW). The differential distribution of enamel thickness is related to an enhanced reliance on shearing stresses in *Homo* and proportionally more crushing and grinding activity in *Pongo*. These observations support previous inferences of tooth function based on biomechanical appraisals of occlusal geometry, and suggest that analyses of enamel thickness patterning can make important contributions to our understanding of the relationship between dietary patterns and enamel thickness in extant hominoid teeth and for generating more refined models of tooth function in early hominins. Furthermore, the success of enamel thickness patterning for discriminating among hominoid molars indicates that this feature may be used for taxonomic purposes, with some success for early fossil hominins.

Though the complicated three-dimensional structure of mature enamel and the overall processes of tooth morphogenesis are well-understood, the genetic mechanisms underlying final tooth size and shape, including enamel thickness, are not. Given that changes in enamel thickness can be brought about by differential rates of ameloblast

activity and secretion, an understanding of the developmental program responsible for odontogenesis has enormous bearing on interpreting the final form of the tooth, in particular, enamel thickness and its relation to tooth function. The ultimate shape of the crown is the result of two independent growth processes: the daily incremental secretion rate of ameloblasts, and the differentiation and extension rate of new cervical ameloblasts; the former refers to the rate of enamel protein gene expression, and the latter is a measure of the number of newly activated ameloblasts along the cervical margin. From previous work, and work in progress, it seems clear that differences in the achievement of adult morphology (i.e., the degree of enamel thickness) are evident among large-bodied extant hominoids. Future work should focus on combining developmental and morphological data on enamel thickness at functionally important regions of the crown as well as in nonfunctional regions of the crown, such as the canine cusp tip, among hominoid species or even between genders (e.g., Schwartz and Dean, 1999).

ACKNOWLEDGMENTS

I thank Glenn Conroy, Chris Dean, Tab Rasmussen, Charles Hildebolt, Gabriele Macho, Lawrence Martin, Don Reid, Peter Shellis, Richard Smith, Jane Phillips-Conroy, Francis Thackeray, Phillip Tobias, David Beynon, and Richard Brand for their encouragement and support as well as their helpful and insightful comments on earlier drafts of this manuscript. Gabriele Macho of the University of Liverpool, Margit Berner of the National History Museum in Vienna, and Lawrence Martin of SUNY Stony Brook kindly allowed use of the modern human and extant hominoid material. This paper benefited greatly from the comments of David Pilbeam and one anonymous reviewer.

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